The Role of Behavioral Traits in Influencing the Distribution of Two Species of Sea Mussel, *Mytilus edulis* and *Mytilus californianus*

BY

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(3 Text figures)

INTRODUCTION

In the course of an investigation into the nature of competitive interactions between two species of sea mussels (*Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837) on the coast of Southern California, I discovered that in addition to certain morphological characters which served to differentiate the two species, a difference in behavior was also apparent. Knowledge of this behavior enabled me to account for a difference in the distribution of the two species in large mussel clumps occurring intertidally on pier pilings. The pier concerned (property of Signal Oil & Gas Company) is located at Ellwood, some 14 miles west of the city of Santa Barbara, California, on an open sandy shore. It is constructed from steel girders and is about half a mile long; the pilings support clumps of mussels in the intertidal region, which range in size from a few individuals up to giant masses some 17 feet (5.2 m) in circumference with a vertical extent of around 9 feet (2.7 m).

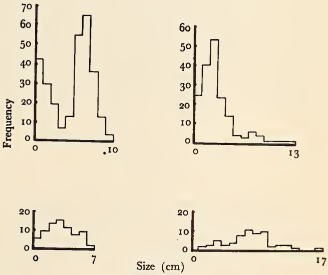

Figure 1

Size distribution of *Mytilus edulis* and *Mytilus californianus* from the inside and outside of a mussel clump at Ellwood Pier. The total sample represents approximately one third (by volume) of a clump measuring 7 feet (2.13 m) in cricumference.

Diagram 1: *Mytilus edulis* from outside the clump. Sample size is 262, mean is 4.6 cm

Diagram 2: *Mytilus edulis* from inside the clump. Sample size is 72, mean is 3.5 cm

Diagram 3: *Mytilus californianus* from inside the clump. Sample size is 175, mean is 3.10 cm

Diagram 4: *Mytilus californianus* from outside the clump. Sample size is 53, mean is 7.82 cm

The class interval for each histogram is 1.0 cm.

A. FIELD INVESTIGATION

METHODS

I investigated the distribution of the two species of mussels within the mussel clumps in the following manner. Before removing samples of mussels from the clumps on the pilings, I sprayed the outside animals thoroughly with white enamel paint. This provided an objective

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Table 1

Numbers of *Mytilus edulis* and *Mytilus californianus* from the inside and outside portions of a sample taken from a mussel clump containing both species. The sample represents approximately one third (by volume) of a clump measuring 7 feet (2.13 m) in circumference.

	Outside		Inside	
	Mytilus californianus	*Mytilus edulis*	*Mytilus californianus*	*Mytilus edulis*
Top	68	117	317	72
Middle	168	555	687	302
Bottom	73	262	343	114

method for determining whether a particular mussel came from inside or outside a cluster. Mussels completely or partly covered with paint were recorded as "outside" mussels and the rest as "inside" mussels (hereafter the term "inside" mussels refers to animals selected in this manner). The mussels were detached by taking a straight hoe and slicing the inside individuals away from a piling face, from the top to the bottom of the aggregation. In this way, a sample of $\frac{1}{4}$ to $\frac{1}{2}$ of the complete clump was removed at one time. I then divided the slab of mussels into 3 equal portions: top, middle, and bottom. Individual mussels of each species then were classified into 6 categories.

e. g.:

Type	*Mytilus californianus*	or	*Mytilus edulis*	
Position	Outside	or	Inside	
Depth	Top,	Middle	or	Bottom

RESULTS of FIELD INVESTIGATION

Table 1 records the number and positions of mussels within $\frac{1}{3}$ of a clump measuring 7 feet (2.1 m) in circumference. In mixed aggregations most of the *Mytilus edulis* occur on the outside of the clumps. *Mytilus edulis* juveniles (up to 2.5 cm) tend to be found on the outside of the clumps while *M. californianus* juveniles tend to occur within the body of the clump. Figure 1 illustrates this distribution.

B. LABORATORY INVESTIGATION

METHODS and RESULTS

For the sake of convenience I will include experiments carried out in the field under the above heading (experiments of this nature were carried out at Ellwood Pier and in the Santa Barbara Harbor).

In the course of studying competition among juvenile mussels (1 - 2 cm in length), I assembled cages containing *Mytilus edulis* mixed evenly with *M. californianus* (100 individuals of each species). These cages were suspended beneath Ellwood Pier below low water level.

At the first inspection of this experiment (after an immersion interval of 1 month) evidence implying a difference in behavior between the two species was revealed. Most of the *Mytilus edulis* in the cages had moved to the outside of the enclosed clumps, leaving the *M. californianus* in the center. Such a difference in behavior would plainly be of advantage for *M. edulis* in a competitive situation since it would seem reasonable to assume that mussels on the outside of a clump would be the first to capture food particles from the surrounding water and, in addition, would not be pressed upon, and therefore interfered with, by their neighbors. This implied difference in behavior suggested a mechanism which would account for the disparate clump distribution shown by the two mussel species. It seemed reasonable to suppose that any *M. edulis* individuals settling within the matrix of a cluster would move to the outside, attach firmly, and then grow to maturity.

To test the possibility of such a difference in behavior between the two species I took small individuals (1 - 2 cm) of both species into the laboratory, placed them (separately) about 5 cm below the surface of road gravel (0.5 to 0.75 cm diameter) within perforated plastic containers and immersed these containers in running sea water. Figure 2 records the cumulative numbers of mussels appearing on the surface of the gravel with the passing of time. *Mytilus edulis* obviously crawls out from the gravel at a much higher rate of speed than does *M. californianus*.

When individuals of *Mytilus edulis* were placed 5 cm below the surface of a gravel filled plastic tube (1.5 inches [3.81 cm] in diameter) which was sealed at one end, they always crawled through the gravel, towards and out of the open end of the tube, regardless of whether

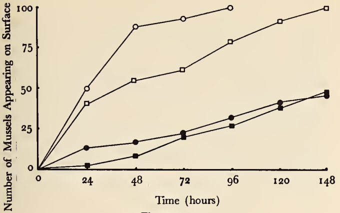

Figure 2

Comparison between the rate of "crawling out" by *Mytilus edulis* and *Mytilus californianus* when both species are initially buried under 5 cm of road gravel.

Two replicate runs for each species are recorded. Solid symbols represent *Mytilus californianus*, open symbols represent *Mytilus edulis*. The total number of animals used for each trial was 100.

the opening faced directly upwards, horizontally or at any intermediary angle.

If small mussels (1 - 2 cm) are buried in gravel at a depth greater than 13 cm, very few of them are able to crawl to the surface, presumably because the weight of the stones is too great for them to move against. This probably helps to explain why the mussels crawled towards the open end of the tube rather than the closed end.

Initially I had thought that small *Mytilus edulis* might settle within the matrix of the clump of mussels and then crawl to the outside using light as a possible orientation cue. To test this hypothesis I placed 3 cages containing small mussels at a depth of 5 cm below the gravel surface, inside light-tight boxes through which ran sea water The first cage was illuminated from the top by a directional light beam, the second was illuminated from the side and the third was kept completely dark. All mussels crawled to the top of the cages and no difference in "crawl-out" rate could be detected among the 3 treatments. This indicated that it was not a positive reaction to light which caused *Mytilus edulis* to orient themselves on the outside of the mussel clumps.

This "crawling-out" reaction, then, seems to be evoked in response to some tactile sensation induced by the pressure of objects resting against the mussels. This hypothesis is supported by the fact that when small *Mytilus edulis* are placed separately within the interstices of a cairn of "fist-sized" stones in such a manner that they press neither against themselves nor against the stones, they do not crawl out (except for an occasional individual), but remain fixed in one place.

The only other mussel to occur in large numbers on the coast of Southern California is *Septifer bifurcatus* (Conrad, 1837), a rather small animal (maximum size 3.5 to 4.5 cm), found only on exposed shores. The crawling behavior of *Septifer* is quite different from that of *Mytilus edulis* or *M. californianus*. When *Septifer* is placed a few centimeters below a gravel surface it dos not move from its position. When placed on top of a bed of gravel or on a pitted surface, *Septifer* reacts by drawing itself down into any depression which it may encounter.

Septifer is generally found in the mid-intertidal area where it nestles in nooks and crannies. Where all 3 species of mussels occur together, *Septifer* is to be found right next to the rock face. *Mytilus californianus* is next, on top of *Septifer,* and finally, *M. edulis* occurs on the outside of such a "three species" clump.

If one considers the two extremes of exposure to wave impact to which *Mytilus edulis* and *M. californianus* are separately adapted, the behavioral differences can be correlated with a presumed advantage for each species. In quiet waters, where *M. edulis* predominates, mussel clumps tend to become saturated with fine mud which settles out from the still water. Table 2 records the mean dry weight of silt taken at bi-monthly intervals from cages immersed in Santa Barbara Harbor (heavy silting), and Ellwood Pier (less silt). Plainly it would be advantageous for any individual to be able to crawl above this mud and so avoid being buried.

Table 2

Comparison of the dry weight of silt taken from cages of mussels set at Santa Barbara Harbor and at Ellwood Pier (below low water), at bi-monthly intervals.

	N	Y	S	N	Y	S
1	4	72.13	±43.38	4	6.13	±3.18
2	2	34.80	±22.0	2	6.88	±6.03
3	2	113.40	±55.80	2	8.40	±1.20
4	4	54.45	±14.95	3	3.51	±2.13
5	2	89.75	± 4.5	2	7.04	±5.98

N = sample size Y = mean S = standard deviation

[In this connection it may be noted that when small mussels of both species are grown together within cages suspended in the Santa Barbara Harbor, *Mytilus edulis* crawls to the outside of the clumps, leaving *M. californianus* on the inside to be eventually smothered by the accumulating silt.]

On the exposed coast where *Mytilus californianus* predominates, it would perhaps be advantageous to this animal to attach itself quite firmly to the substratum since any individual crawling to the outside of a clump would presumably run the danger of being washed off. In fact, pure *M. californianus* clumps tend to be very tightly bound up with byssal threads and it is almost impossible to tear chunks of such clumps loose with one's bare hands. In contrast to this, when *M. edulis* forms pure species clusters (i. e., on pilings within harbors), it is possible to tear these clumps apart with little effort. It is as if individuals of *M. edulis* sabotage the structure of the clumps of which they are a part by continually attempting to crawl out on top of each other.

An alternative reason for the marked crawling behavior of *Mytilus edulis* might be that this is a "behavioral character displacement" which has been evolved through competition with *M. californianus* (i. e., individuals of *M. edulis* which become trapped within a clump are soon crushed and only those on the outside of a clump may survive).

To throw some light on the latter hypothesis, I took some *Mytilus edulis* from the East Coast of the U. S. A. (Cape Ann, Massachusetts) where *M. californianus* does not occur, and compared their "crawl-out" behavior with

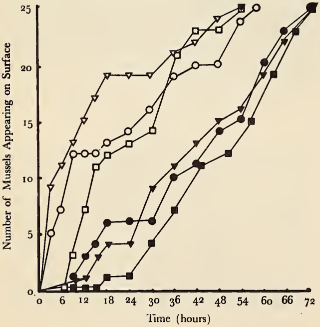

Figure 3

Comparison between the rate of "crawling out" shown by *Mytilus edulis* from the West Coast of North America (Santa Barbara, California) and *Mytilus edulis* from the East Coast of North America (Cape Ann, Massachusetts), when both samples are initially buried under 5 cm of road gravel.
Three replicate runs for each sample are recorded, solid symbols representing West Coast *Mytilus edulis*, open symbols representing East Coast *Mytilus edulis*, with total number of animals used for each trial 25 and the water temperature at 18° C.

that of the West Coast (Santa Barbara) *M. edulis*. The East Coast mussels crawled out from the gravel at a much faster rate than the West Coast mussels (Figure 3). This experiment was repeated in water at temperatures of 12° C and 18° C (the latter was the temperature of Santa Barbara ocean water) with similar results. Since *M. edulis* occurs by itself on the East Coast, it would seem that this behavior might have developed as an adaptation to the physical environment rather than as a response to interspecies competition. If this were so, one could then view "crawling out" behavior as a preadaptation for competitive interaction with *M. californianus*.

DISCUSSION

Crawling behavior of *Mytilus edulis* has been noted by European workers, i. e., Field (1922) and Maas Geesteranus (1942). Field (*op. cit.*) described the course of several small mussels as they worked their way up an aquarium wall. Movement takes place in the following manner: the mussel extends its foot and at the same time produces a byssal thread which it then fastens by means of the foot-groove and associated glands at the tip of the foot, then releasing its old thread(s) and pulling itself onto the new one. The process is then repeated until journeying is done. This characteristic behavioral trait of *M. edulis* is in itself rather insignificant but it is enough to give the animal a considerable advantage when competing with *M. californianus* (Harger, 1967). Of course, the position on the outside of a mussel clump is not entirely without danger, as the likelihood of being swept away by waves or taken by some predator is greatly increased (Harger, *op. cit.*, Landenberger, 1967).

It is possible that it is this "crawling out" behavior which has enabled *Mytilus edulis* to become so widespread throughout the world (see Stubbings, 1954, for an account of the distribution). Certainly *M. edulis* is spread widely throughout the Northern and Southern hemispheres and, further, it is known to successfully colonize both rocky shores and muddy bottomed bays (Lewis, 1953).

It would indeed be interesting to know whether any other species of mussel is as adept at this crawling behavior as *Mytilus edulis*.

SUMMARY

I have shown that a difference in behavior exists between *Mytilus edulis* and *M. californianus* in that the former species tends to crawl more rapidly out from under objects which press against it, than the latter. A third mussel, *Septifer bifurcatus*, does not show this behavior but rather tends to pull itself down against the substratum.

The crawling behavior ensures that *Mytilus edulis* becomes arranged on the outside of mixed species (*M. californianus* and *M. edulis*) mussel clumps and so enjoys an initial competitive advantage over *M. californianus*. This behavior also insures that *M. edulis* can keep above the surface of mud when it colonizes soft muddy areas (bays, etc.).

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